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EXCEPTIONAL EPIPHYTE DIVERSITY ON A SINGLE TREE IN COSTA RICA

ERIC SCHUETTPELZ*

Department of Biology, Duke University, Durham, NC 27708, USA. Email: ejs7@duke.edu

DORSET W. TRAPNELL

Department of Plant Biology, University of Georgia, Athens, GA 30602, USA.
Email: dorset@plantbio.uga.edu

ABSTRACT. An exhaustive survey of vascular epiphytes on a single mature canopy tree in a Costa Rican tropical premontane wet forest revealed an extraordinary level of epiphyte diversity. A total of 126 morphospecies representing at least 52 genera and 21 plant families were found growing epiphytically on the phorophyte (host tree), accounting for more than 1% of the entire vascular flora of Costa Rica. This is considerably higher than most other epiphyte surveys of single trees. Angiosperms accounted for 64% of the species while leptosporangiate ferns accounted for 36%. Consistent with earlier studies, orchids contributed less than would be expected from their global representation, while ferns contributed more significantly to species diversity. Fewer species were found on the tree trunk (58 species) than in the crown (85 species), and little species overlap occurred between these two regions (17 species), suggestive of niche partitioning. Three species and 11 individuals per m^2 were recorded on the trunk of the phorophyte. Our results underscore the important contributions of epiphytes to overall biodiversity, and highlight the necessity of including epiphytes in future biodiversity assessments.

Key words: biodiversity, neotropical premontane wet forest, vascular epiphytes

INTRODUCTION

Epiphytism, which has been documented in 84 vascular plant families, apparently evolved independently many times (Kress 1986). Epiphytes contribute substantially to global plant diversity (Schimper 1888, Madison 1977, Dressler 1981, Kress 1986, Gentry & Dodson 1987a, Nieder et al. 2001), accounting for ca. 10% of all vascular plant species (Kress 1986). In tropical and subtropical regions, where the potential for environmental stress is greatly alleviated by consistently high moisture levels, epiphytes are a particularly important component of floral diversity. The contributions of epiphytic species in the neotropics can be especially high (Richards 1957, Madison 1977, Gentry & Dodson 1987b). In Ecuador, for example, epiphytes account for more than 25% of the total vascular flora (Møller Jørgensen & León-Yánez 1999). Despite representing a significant component of plant diversity, epiphytes often are overlooked in community diversity assessments. Such inventories traditionally focused on terrestrial woody taxa, and this bias has resulted in an incomplete and inaccurate understanding of biodiversity in many regions. With the steady rise of habitat destruction, the need for a more comprehensive approach to biodiversity assessment has become increasingly apparent.

The relatively few investigations to date that included both terrestrial and epiphytic taxa have provided invaluable insights. They have demonstrated that, in some tropical forest communities, epiphytes may compose more than 50% of the vascular plant species (Kelly et al. 1994), and they have revealed that the relative proportion of epiphytes, commonly called the epiphyte quotient (Hosokawa 1950), is scale dependent (Ibisch et al. 1996; Nieder et al. 1999, 2001). Considerably higher epiphyte quotients are found at smaller scales than at larger scales, and while sampling at any scale, the number of epiphytic species will approach saturation much sooner than the number of terrestrial species. High epiphyte diversity within an especially small area thus would be expected; and, indeed, as many as 195 epiphytic species have been documented from a single tree (Catchpole 2004).

The objective of our study was to further explore epiphytic species richness by conducting a complete survey of vascular epiphytes on a single canopy tree in a Costa Rican tropical premontane wet forest. This additional data on epiphyte diversity may underscore the role of epiphytes in biodiversity and further emphasize the necessity of including epiphytes in future assessments. With increased habitat disturbance, epiphyte diversity and abundance decline substantially (Barthlott et al. 2001), and species composition is altered. Considering the ubiqui-

* Corresponding author.

TABLE 1. Taxonomic and spatial distribution of vascular epiphytes collected from a single canopy tree in a Costa Rican tropical premontane wet forest.

	Angiosperm		Fern		Total	
Location	Species	Families	Species	Families	Species	Families
Trunk only	24	3	17	1	41	4
Crown only	47	4	21	1	68	5
Trunk and crown	10	6	7	6	17	12
Total	81	13	45	8	126	21

Note: Taxonomy follows that of the Instituto Nacional de Biodiversidad (INBio), Costa Rica (http://www.inbio.ac.cr/).

tous nature of human-induced habitat disturbance, the need for information concerning the contributions of epiphytic taxa and the distribution of epiphytic diversity is ever more urgent.

MATERIALS AND METHODS

The single-tree survey was conducted at the Reserva Biológica Alberto Brenes, situated in tropical premontane wet forest (at ca. 1000 m with ca. 4000 mm annual precipitation) on the Atlantic slope of Costa Rica in June 2002. A recently fallen (<5 days prior to the survey) mature canopy tree was selected to allow unrestricted and comprehensive epiphyte sampling. The phorophyte (host tree), identified as *Pseudolmedia mollis* Standl. (Moraceae), was ca. 30 m tall with a diameter at breast height (dbh) of 0.64 m, comparable to other mature trees in the surrounding forest. The trunk (measured from the ground to the first major ramification) accounted for ca. 11 m of total height, and the crown (from the first major branch upward) accounted for ca. 19 m. All vascular epiphytes were collected from the trunk to facilitate a description of epiphyte diversity, abundance, and density on this portion of the tree. From the crown, representatives of each morphologically distinct taxon were collected, without consideration of abundance or density because the crown partially shattered when the tree fell, precluding accurate assessment. All collections were sorted and identified to the lowest possible taxonomic rank. Many collections were sterile; therefore, not every individual could be assigned a species name. Such individuals were evaluated relative to other named and un-named individuals to assess whether or not they represented unique taxa. Juvenile plants, not assignable to a mature collection or not distinct from the other collections, were excluded from the study. Voucher specimens corresponding to each taxon were deposited at the Museo Nacional de Costa Rica (CR), see APPENDIX.

RESULTS AND DISCUSSION

At first glance, the study tree appeared somewhat depauperate of vascular epiphytes. Its bark was relatively smooth and unfurrowed and, compared to many of the canopy trees standing in the forest, its epiphyte load initially appeared somewhat disappointing. Upon completion of the survey, however, 126 morphospecies representing at least 52 genera and 21 families were found growing epiphytically on the tree (TABLE 1, APPENDIX). All but three morphospecies were identified to family, and 117 were identified to genus. Time constraints prevented cultivation of unassigned individuals, and only 57 taxa could be assigned to named species. Nonetheless, indications are that most, if not all, of the 126 taxa represent true species. This result reveals an exceptional diversity of epiphytes at a reduced spatial scale (i.e., a single phorophyte). The number of epiphytic taxa supported by this single tree represents more than 1% of the entire vascular flora of Costa Rica (Obando 2002). Although Costa Rica is an admittedly small country, its unique geographic features have given rise to a variety of habitats that lie in close proximity to one another. Flanked by two oceans, the country's climate is strongly influenced by oceanic winds and currents from the Caribbean and the Pacific Ocean. Furthermore, the country is bisected by three cordilleras (elevations from sea level to 3820 m) with adjacent slopes in different orientations. These physical features have given rise to an unusually large number of distinct habitats, from very dry to very wet, which in turn have contributed to extraordinary levels of biodiversity.

The number of species documented by this single-tree study in Costa Rica is considerably higher than numbers reported in most other single-tree epiphyte surveys. Previous investigations have uncovered up to 41 epiphytic species on a single tree in Southeast Asia (Went 1940) and up to 45 species on a single tree in Africa

(Biedinger & Fisher 1996). In the neotropics, the documented numbers are generally higher, but only up to 72 species from a single tree in French Guiana (Freiberg 1999), 107 from a single tree in Mexico (Valdivia 1977), and 109 from a single tree in Ecuador (Nowicki 1998). To date, just one available study has reported a higher number of epiphyte species from a single tree; Catchpole (2004) found 195 vascular epiphyte species on an emergent canopy tree in a Peruvian cloud forest.

Of the 126 taxa occupying the Costa Rican study tree, angiosperms accounted for 64% (81 species), and leptosporangiate ferns accounted for 36% (45 species, see TABLE 1). Other vascular plant lineages were not found. The Orchidaceae, Araceae, and Lomariopsidaceae were the most species-rich families on the phorophyte (with 25, 20, and 15 species, respectively). The remaining families were each represented by ≤8 species (APPENDIX). Orchids and ferns are the predominant vascular epiphytes nearly everywhere (Gentry & Dodson 1987b), and this was certainly true on the Costa Rican study tree; together, orchids and ferns accounted for more than half the species observed. On the scale of this one phorophyte, however, we found substantial departures from the contributions of these taxa on a global scale. Worldwide, orchids compose the most strikingly diverse group of epiphytes (Gentry & Dodson 1987b). More than 70% of orchid species are epiphytic, and these account for ca. 60% of all vascular epiphytes—ten times as many as any other vascular plant family (Kress 1986). The mere 20% contribution of orchids on the study tree represents a significant departure from the global figure, but this is consistent with the observation that orchids generally occur in low densities in undisturbed tropical forests (Nieder et al. 1999, Koopowitz 2001). Orchids are generally rare, and sampling on the scale of a single tree is unlikely to accurately reflect their forest-wide species richness; therefore, larger scale surveys are needed. Worldwide, ferns account for more than 10% of the epiphyte species (Kress 1986); however, on our study tree, they comprised 36% (45 species) of the epiphytic species. Although skewed, these numbers are in agreement with reports that epiphytic ferns are more evenly distributed and thus contribute more dramatically to species diversity at smaller spatial scales (Nadkarni 1985, Hietz & Hietz-Seifert 1995a, Nieder et al. 1999).

A comparison of epiphytes sampled from the two partitions of the phorophyte revealed that the trunk harbored considerably fewer species (58 species) than did the crown (85 species; TABLE 1). Little species overlap occurred between these two regions of the tree, with only 13% (17 species) of the species found growing in both (TABLE 1). At the family level, however, substantial overlap did occur, with 12 of 21 families found in both the trunk and crown partitions. Even so, four families occurred exclusively on the trunk (Begoniaceae, Dryopteridaceae, Marcgraviaceae, and Urticaceae), and five families were restricted to the crown (Araliaceae, Clusiaceae, Ericaceae, Oleandraceae, and Rubiaceae). Other plant families showed biases toward one partition or the other of the study tree (e.g., Bromeliaceae and Orchidaceae tended to be more prevalent in the crown; APPENDIX). Although these data from a single tree are based on a qualitative rather than quantitative assessment, they do support the notion of some degree of within-tree niche partitioning. This is consistent with the results of earlier studies that have evaluated the vertical distribution of epiphytes (Johansson 1974, Gentry & Dodson 1987b, ter Steege & Cornelissen 1989, Hietz & Hietz-Seifert 1995b, Freiberg 1996). Because of the general tendency for epiphytic species to occupy various positions within a tree (Hietz & Hietz-Seifert 1995b); however, comprehensive sampling of multiple trees is necessary to identify the true extent and precise nature of any niche partitioning.

Species and plant density were assessed only for the trunk, since the crown shattered partially when the tree fell, precluding accurate assessment. On the tree trunk, 239 epiphytes belonging to 58 species were collected. This represents a density of ca. three species and 11 individuals per m^2 (based on an estimated surface area of 22 m^2 calculated from height and dbh; see APPENDIX). Ferns occurred at higher individual densities on the tree trunk than did angiosperms, accounting for 59% of the individuals but only 41% of the species, further supporting the notion that ferns occur at higher densities in forests than do other epiphytes. Only six taxa were represented by ≥10 individuals on the trunk: five ferns (*Asplenium auriculatum, Asplenium pteropus, Campyloneurum sphenodes, Elaphoglossum erinaceum,* and *Pecluma* sp. 1) and one angiosperm (*Pilea diversissima*; APPENDIX).

CONCLUSION

The results presented here reveal an extraordinary level of epiphyte diversity on a single phorophyte and further underscore the significant contributions of epiphytes to overall biodiversity levels. Although the study observations were limited to one tree, the small-scale patterns observed in many ways echoed the small- and even large-scale patterns documented in earlier studies. The geographic distribution of epiphytic diversity, however, is still not fully understood.

Clearly environmental moisture and altitude both play key roles (Gentry & Dodson 1987a, 1987b; Ibisch et al. 1996; Nieder et al. 1999), but just how closely the distribution of epiphytic diversity mirrors that of more commonly sampled woody terrestrial taxa remains to be seen. For now, accurate appraisals of biodiversity and effective conservation policy decisions in these times of increasing habitat disturbance and destruction mandate the inclusion of epiphytes in biodiversity surveys.

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APPENDIX. Spatial distributions of vascular epiphyte species collected from a single canopy tree in a Costa Rican tropical premontane wet forest.

Taxon	Trunk	Crown	Voucher
Angiosperms			
Araceae			
Anthurium sp. 1	1	+	106
Anthurium sp. 2	−	+	107
Anthurium sp. 3	−	+	108
Anthurium sp. 4	−	+	109
Anthurium sp. 5	−	+	110
Anthurium sp. 6	1	−	111
Anthurium sp. 7	2	−	112
Anthurium sp. 8	3	−	113
Monstera sp. 1	1	−	105
Philodendron sp. 1	5	−	114
Philodendron sp. 2	1	−	115
Philodendron sp. 3	1	−	116
Philodendron sp. 4	1	+	117
Philodendron sp. 5	2	−	118
Philodendron sp. 6	7	−	119
Philodendron sp. 7	−	+	120
Philodendron sp. 8	−	+	121
Philodendron sp. 9	1	+	122
Stenospermation sp. 1	−	+	103
Stenospermation sp. 2	−	+	104
Araliaceae			
Schefflera sp. 1	−	+	81
Begoniaceae			
Begonia sp. 1	1	−	74
Begonia sp. 2	4	−	75
Bromeliaceae			
Guzmania sp. 1	4	+	95
Guzmania sp. 2	−	+	96
Pitcairnia sp. 1	−	+	100
Tillandsia sp. 1	−	+	98
Vriesia sp. 1	−	+	97
Vriesia sp. 2	−	+	99
Indetermined sp. 1	−	+	−
Clusiaceae			
Indet. sp. 1	−	+	76
Ericaceae			
Cavendishia complectens Hemsl.	−	+	77
Indet. sp. 1	−	+	78
Indet. sp. 2	−	+	79
Indet. sp. 3	−	+	80
Gesneriaceae			
Columnea cf. *microphylla* Klotzsch & Hanst. ex Oer	1	+	92
Drymonia sp. 1	1	−	93
Indet. sp. 1	−	+	94
Marcgraviaceae			
Marcgravia sp. 1	1	−	73
Melastomataceae			
Blakea litoralis L.O.Williams	7	+	69
Blakea sp. 1	1	−	71
Blakea sp. 2	1	+	72
Centradenia inaequilateralis (Schltdl. & Cham.) G.Don	2	−	70
Orchidaceae			
Chondrorhyncha reichenbachiana Schltr.	2	−	58
Dichaea sp. 1	1	−	60
Elleanthus cf. *caricoides* Nash	−	+	44
Elleanthus cf. *lentii* Barringer	−	+	45
Elleanthus sp. 1	−	+	50

APPENDIX. Continued.

Taxon	Trunk	Crown	Voucher
Epidendrum sp. 1	–	+	56
Epidendrum sp. 2	–	+	–
Malaxis sp. 1	1	–	62
Masdevallia nidifica Rchb. f.	–	+	101
Maxillaria brunnea Linden & Rchb. f.	–	+	49
Maxillaria cf. bradeorum (Schltr.) L.O.Williams	–	+	46
Maxillaria confusa Ames & C.Schweinf.	1	+	48
Maxillaria fulgens (Rchb. f.) L.O.Williams	–	+	43
Maxillaria reichenheimiana Rchb. f.	–	+	47
Pleurothallis sp. 1	–	+	55
Prosthechea cf. *pygmaea* (Hook.) W.E.Higgins	–	+	40
Prosthechea vespa (Vell.) W.E.Higgins	–	+	39
Scaphyglottis sp. 1	1	+	61
Sobralia sp. 1	–	+	–
Stelis sp. 1	–	+	52
Stelis sp. 2	–	+	53
Stelis sp. 3	–	+	51
Stelis sp. 4	–	+	42
Stelis sp. 5	–	+	41
Stelis sp. 6	–	+	102
Piperaceae			
Peperomia sp. 1	3	–	86
Peperomia sp. 2	8	–	87
Peperomia sp. 3	1	–	88
Peperomia sp. 4	5	+	89
Peperomia sp. 5	–	+	90
Peperomia sp. 6	2	–	91
Sarcorachis naranjoana (C. DC.) Trel.	–	+	85
Rubiaceae			
Cosmibuena sp. 1	–	+	82
Urticaceae			
Pilea diversissima Killip	20	–	83
Pilea ptericlada Donn.Sm.	4	–	84
Indet.			
Indet. sp. 1	–	+	123
Indet. sp. 2	–	+	124
Indet. sp. 3	–	+	125
Ferns			
Aspleniaceae			
Asplenium auriculatum Sw.	22	–	126
Asplenium cuspidatum Lam.	1	+	17
Asplenium maxonii Lellinger	–	+	37
Asplenium pteropus Kaulf.	14	–	127
Asplenium serra Langsd. & Fisch.	–	+	38
Dryopteridaceae			
Dryopteris patula (Sw.) Underw.	1	–	131
Polybotrya alfredii Brade	2	–	132
Grammitidaceae			
Enterosora trifurcata (L.) L.E.Bishop	–	+	19
Melpomene anfractuosa (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran	3	–	133
Micropolypodium cf. *taenifolium* (Jenman) A.R.Sm.	–	+	35
Terpsichore alsopteris (C.V.Morton) A.R.Sm.	–	+	36
Hymenophyllaceae			
Hymenophyllum fucoides (Sw.) Sw.	–	+	143
Hymenophyllum polyanthos (Sw.) Sw.	–	+	145
Hymenophyllum saenzianum L.D.Gomez	–	+	144
Trichomanes cf. *reptans* Sw.	4	–	140
Trichomanes collariatum Bosch	1	–	141
Trichomanes diaphanum Kunth	1	+	142
Trichomanes sp. 1	3	–	146

APPENDIX. Continued.

Taxon	Trunk	Crown	Voucher
Lomariopsidaceae			
Elaphoglossum auripilum H.Christ	−	+	31
Elaphoglossum cf. *latifolium* (Sw.) J.Sm.	2	−	129
Elaphoglossum cf. *smithii* (Baker) H.Christ	−	+	27
Elaphoglossum ciliatum T.Moore	−	+	26
Elaphoglossum doanense Gomez	4	+	33
Elaphoglossum erinaceum (Fée) T.Moore	11	+	29
Elaphoglossum grayumii Mickel	3	−	128
Elaphoglossum lanceiforme Mickel	−	+	28
Elaphoglossum lingua (C.Presl) Brack.	−	+	24
Elaphoglossum palmense H.Christ	−	+	25
Elaphoglossum peltatum (Sw.) Urb.	−	+	32
Elaphoglossum phoras Mickel	1	−	130
Elaphoglossum setosum (Libem.) T.Moore	2	+	30
Elaphoglossum sp. 1	−	+	23
Elaphoglossum sp. 2	−	+	22
Oleandraceae			
Nephrolepis pectinata (Willd.) Schott	−	+	34
Polypodiaceae			
Campyloneurum angustifolium (Sw.) Fée	1	−	134
Campyloneurum sphenodes (Kunze ex Klotzsch) Fée	16	+	20
Niphidium sp. 1	−	+	−
Pecluma sp. 1	41	+	147
Pleopeltis sp. 1	1	−	138
Polypodium dissimile L.	1	−	137
Polypodium dulce Poir.	1	−	136
Polypodium fraxinifolium Jacq.	−	+	15
Vittariaceae			
Polytaenium cajenense (Desv.) Benedict	1	−	139
Scoliosorus ensiforme (Hook.) T.Moore	4	−	135
Vittaria remota Fée	−	+	18

Note: Taxonomy follows that of the Instituto Nacional de Biodiversidad (INBio), Costa Rica (http://www.inbio.ac.cr/). Integers indicate presence of epiphytes on the trunk and refer to the number of individuals collected; + = presence in the crown; − = absence. Voucher numbers are E. Schuettpelz collection numbers (− = no voucher); voucher specimens are deposited at the Museo Nacional de Costa Rica (CR).